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Environmental stresses do not always adversely affect seedling growth

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Abstract

Excessively high temperatures and droughts after winter dormancy breaking can affect the growth and mortality of seedlings. An open-field experiment was conducted to understand the growth and mortality of *Larix kaempferi* seedlings to spring warming and drought treatments, and further to explore if seedlings could recover the growth capability when the treatments ceased. One-year-old seedlings were subjected to two temperature levels (ambient temperature and infrared heater warming of 4 °C compared to ambient temperature) and two precipitation levels (ambient precipitation and drought) for four weeks. Warming and drought treatments decreased the height and root collar diameter of seedlings throughout the period. After the cessation of treatments, mortality rates continued to increase in the drought-treated plots until the end of the growing season in November; the combination of warming and drought treatments had the highest mortality rates, followed by the drought treatment, the control, and the warming treatment. However, the combination of warming and drought treatments increased the biomass accumulation, seedling height, and root collar diameter at the end of the growing season. This indicates that the reduced number of seedlings per plot due to the increased mortality may reduce the negative effects of warming and drought on seedling growth through alleviating resource competition among seedlings. This study shows the growth of *Larix kaempferi* seedlings could decline under warmer and drier conditions, and such effects are likely to be mitigated by the decreased density due to the increased mortality rates.

Keywords: climate change; drought; growth; *Larix kaempferi*; mortality

Introduction, scope and main objectives

Since 1970 the global average temperature has been rising at a rate of 1.7°C per century, compared to a long-term decline over the past 7,000 years at a baseline rate of 0.01°C per century (IPCC 2018). Warming greater than the global average has already been experienced in many regions and seasons (IPCC 2018). In Seoul, South Korea, the mean air temperature during spring, which was 12.9 °C in 2019, is expected to increase to 16.6 °C by 2100 under the Representative Concentration Pathway (RCP) 8.5 (Korea Meteorological Administration 2020). Furthermore, the Korea Meteorological Administration projected that the maximum number of consecutive dry days would increase from 18 days in 2019 to 30 days by 2100 in Seoul.

Heat and drought are the major stresses influencing plant growth and physiological responses (Li 1998). Excessively high temperatures and droughts after winter dormancy can negatively affect the growth responses such as seedling height, root collar diameter, biomass accumulation, and mortality of seedlings (Lipiec et al. 2013).

Generally, experimental warming and drought studies have been conducted in indoor or open-field experiments (Lee et al. 2013). Numerous indoor experiments were conducted to study plants' response to changes in atmospheric or soil conditions in greenhouses (Ambee et al. 2009; Meyer-Grünefeldt et al. 2015; Kasurinen et al. 2016). In contrast, the previous open-field experiments involved artificially changing atmospheric or soil conditions outdoors using infrared lamps, heat wires, chambers, or precipitation blocking systems to observe plant reactions (Jo et al. 2011; Chung et al. 2013). Despite the difficulties in controlling temperature and precipitation in open-field experiments, these kinds of experiments have the advantage of maintaining other environmental factors (Chung et al. 2013). Moreover, open-field experiments on climate change involving two or more factors are increasing (Wu et al. 2011; Chang et al. 2019).

Larix kaempferi accounts for 36% of the total plantation area in South Korea. This species is a major forest resource for timber production with consistent cultivation in Korea (Korea Forest Service 2020a; 2020b). However, the distribution of coniferous forests in South Korea is expected to decrease rapidly and become endangered with rising temperatures (NIFoS 2014). Trees are relatively sensitive to changes in environmental conditions at the seedling stage because their roots and stems are not fully developed (Fisichelli et al. 2014). Therefore, it is indispensable to study the responses to warming and drought with seedling stage *Larix kaempferi* in the open-field.

Studies on the growth responses of *L. kaempferi* to the warming and drought treatments have been conducted worldwide (Kwon et al. 2020; Han et al. 2012; Bhusal et al. 2020). However, few studies have simulated warming and drought in the spring season only, and few have explored the effects on *L. kaempferi* continuously after the cessation of the warming treatment. Seedlings are more sensitive to environmental stresses in the spring season than the other seasons. It is necessary to understand how excessively high temperatures and drought can affect seedlings during spring and how their response changes when the high-temperature and drought period ends. Therefore, in the present study, we investigated the effects of spring warming and drought on the growth of *L. kaempferi* seedlings until the end of the plant growing season of the year. We hypothesized that the warming and drought treatments would reduce seedling height, root collar diameter, and biomass accumulation and increase mortality rates.

Methodology

1-Experimental warming and drought treatments

The experiment was conducted in open-field conditions in the Korea University Green Campus, Seoul, South Korea (37° 35’ 36’’ N, 127° 1’ 31’’ E). The region is characterized by a temperate climate with a mean annual precipitation of 1450.5 mm (61% occurring from June to August) and a mean annual temperature of 12.5 °C (Korea Meteorological Administration 2020). The soil texture of the study site was sandy loam. The soil acidity (pH), soil carbon concentration (%), and soil nitrogen concentration (%) were 6.52, 0.22, and 0.05, respectively.

The experimental plots were established in March 2020. One-year-old *L. kaempferi* seedlings were subjected to two temperature levels (ambient temperature and infrared heater warming of 4 °C compared to ambient temperature) and two precipitation levels (ambient precipitation and drought) for four weeks. Twenty 1.0 m × 1.5 m plots were established for each of the four treatments with five replicates: control (TC*PC), drought (TC*PD), warming (TW*PC), and the warming and drought treatments combined (TW*PD). Eighty *L. kaempferi* seedlings were planted in each plot. The warmed plots were heated for seven days each in the second and fourth weeks of May 2020 by an infrared heater suspended 60 cm above the average seedling height. In the temperature control plots, a dummy of the same shape and size as the infrared heater was suspended 60 cm above the average seedling height to simulate the shading effects of the heater. The drought treatment was consisted of full rain exclusion by suspending automatic rain-out shelter at a height of 1.6 m above the soil. The rain-out shelters were coiled on a beam and automatically operated by an electronic controller as it detects rain. The ambient control plots remained without climate manipulation throughout the entire manipulation period. To monitor the air temperature, soil temperature, and soil moisture content, infrared thermometers (SI-111, Campbell Scientific Inc., USA) and soil temperature·moisture sensors (CS655, Campbell Scientific Inc., USA) were installed in each plot. Environmental data were collected each half-hour using a data logger.

2-Seedling growth and mortality rate

Seedling height and root collar diameter of all seedlings were measured on April 30, June 1, and October 30, 2020. Seedling height was measured by the folding ruler. Root collar diameter was measured by the digital caliper at a height of 1 cm above the ground. At the end of the growing season, five randomly selected seedlings were collected from each plot and the total biomass was recorded. These seedlings were excavated by hand to recover as many roots as possible. The harvested seedlings were partitioned into stem, leaves, and roots, dried at 65 °C, and weighed to the nearest 0.01 g. During the growing season, the mortality rate was quantified monthly.

3-Data analysis

Repeated-measures ANOVA and two-way ANOVA were performed to analyze the effect of artificial warming, drought, and their interaction on each of the dependent variables. Individual treatments were compared with Tukey’s test to identify whether they were significantly different at the 0.05 probability level. All statistical analyses used SAS version 9.4 statistical software (SAS Institute Inc., USA).

Results

1-Experimental warming and drought treatments

Warming, drought, and time had significant effects on air temperature, soil temperature, and soil moisture content (Table 1). During the warming treatment period (second week and fourth week of May 2020), compared with TC*PC, warming and drought elevated air temperature by 0.99, 4.04, and 4.86 °C in TC*PD, TW*PC, and TW*PD, respectively (Fig. 1a). During the warming treatment period, soil temperature was also significantly increased by 1.84, 4.97, and 6.43 °C in TC*PD, TW*PC, and TW*PD relative to TC*PC by the warming and drought treatments, respectively (Fig. 1b). Warming and drought treatments decreased mean soil moisture content by 52.01, 15.10, and 63.17 vol % in TC*PD, TW*PC, and TW*PD, respectively, compared with TC*PC (Fig. 1c).

Table 1: Results of repeated-measures ANOVA for the effects of warming, drought, and time on environmental and growth responses of *Larix kaempferi* seedlings.

Effect	AT	ST	SMC	SH	RCD	M
W	**511.11*****	**2032.04*****	**1316.22*****	0.01	**12.26*****	**14.59*****
D	**27.12*****	**276.35*****	**17111.40*****	**14.46*****	**8.57****	**81.36*****
T	**942.85*****	**2584.16*****	**3754.06*****	**1592.99*****	**1262.79*****	**13.37*****

W×D	0.60	1.36	**5.71***	**44.86*****	**4.25***	**39.83*****
W×T	**162.56*****	**693.23*****	**153.36*****	1.44	1.61	0.07
D×T	**11.5*****	**84.26*****	**2414.31*****	2.16	**17.87*****	**2.75*****
W×D×T	0.01	0.71	**36.83*****	**33.47*****	**5.69****	0.86

W, warming treatment; D, drought treatment; T, times; AT, air temperature; ST, soil temperature; SMC, soil moisture content; SH, seedling height; RCD, root collar diameter; M, mortality. Bold type indicates significant differences (*$p < 0.05$; **$p < 0.01$: ***$p < 0.001$).

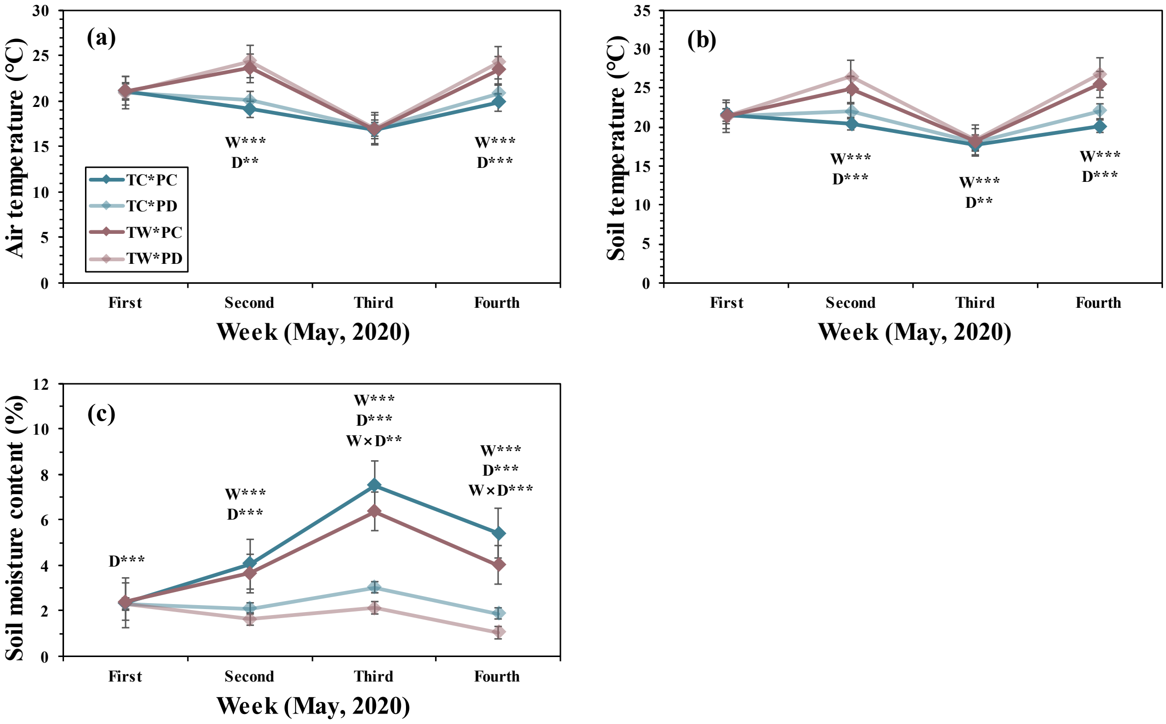

Fig. 1: Mean weekly changes in (a) air temperature, (b) soil temperature, and (c) soil moisture content in May 2020. Error bars are the standard errors of the means, and asterisk (*) symbols indicate significant differences by the warming and drought treatments, respectively (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$). Treatments are as follows: TC*PC, control; TC*PD, drought; TW*PC, warming; TW*PD, warming and drought treatments combined.

2-Seedling growth response

Overall, the warming and drought treatments significantly affected seedling height, root collar diameter, and biomass accumulation, and there was a significant interaction between the warming and drought treatments (Table 1). Immediately after the treatments, the seedling height was influenced by the drought treatment and the interactive effects of warming and drought treatments, whereas root collar diameter was influenced by each warming and drought treatment (Fig. 2). The initial seedling height was 30.28 ± 6.95 cm, and immediately after the treatments, the highest values were observed in TC*PC (32.66 ± 5.24 cm) and the lowest values were observed in TW*PD (31.34 ± 6.93 cm) (Fig. 2a). The initial root collar diameter was 3.97 ± 0.84 mm, and immediately after the treatments, the highest values were observed in TC*PC (4.59 ± 0.71 mm) and the lowest values were observed in TW*PD (4.22 ± 0.59 mm) (Figure 2b). After the cessation of treatment, TW*PD, which was the smallest in both seedling height and root collar diameter, gradually increased over time and showed values as high as TC*PC at the end of the growing season in October. The leaf, shoot, and total biomass accumulation were considerably greater in TW*PD than in the other treatments (Fig. 3).

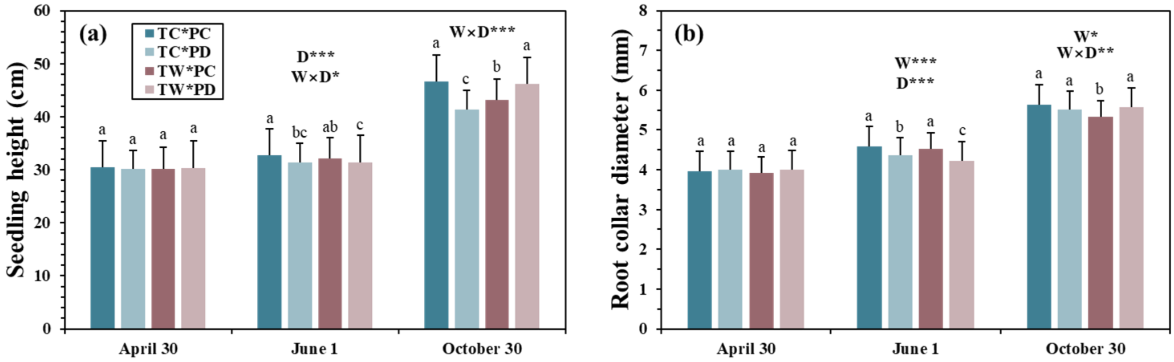

Fig. 2: Seedling height (a) and root collar diameter (b) of *Larix kaempferi* seedlings in 2020. Abbreviations of the plots are in Fig. 1. Bars with different letters are significantly different among treatments at the $p < 0.05$. Error bars are the standard errors of the means, and asterisk (*) symbols indicate significant differences by the warming and drought treatments, respectively (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

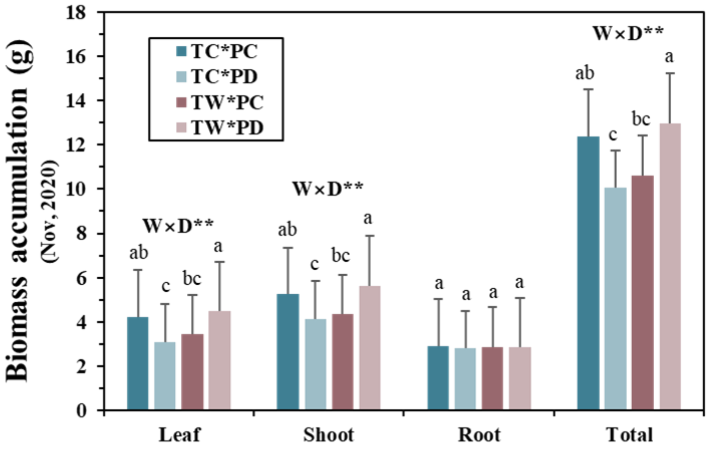

Fig. 3: Biomass accumulation of *Larix kaempferi* seedlings as influenced by warming and drought treatments. Abbreviations of the plots are in Fig. 1. Bars with different letters are significantly different among treatments at the $p < 0.05$. Error bars are the standard errors of the means, and asterisk (*) symbols indicate significant differences by the warming and drought treatments, respectively (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

3-Mortality rate

From September, the mortality rate was significantly increased by drought, while no significant differences were detected until August. However, there was no significant effect of warming and interactive effect of warming and drought treatments on the mortality rate of seedlings in individual months. The final mortality

(%) in November 2020 was 4.00 in TC*PC, 5.60 in TC*PD, 1.87 in TW*PC, and 9.07 in TW*PD, respectively (Fig. 4). At the end of the growing season, TW*PD had the highest mean value for the growth but also experienced the highest mortality rate (Fig. 4). The final mortality significantly increased by 2.50-fold under the drought treatment. In monthly data, only the effect of the drought treatment was found to be significant, but in the overall data, there were also significant effects of warming and interaction effect with drought (Table 1). Seedling mortality rate under the drought treatment gradually increased until August, and rapidly increased from August to October.

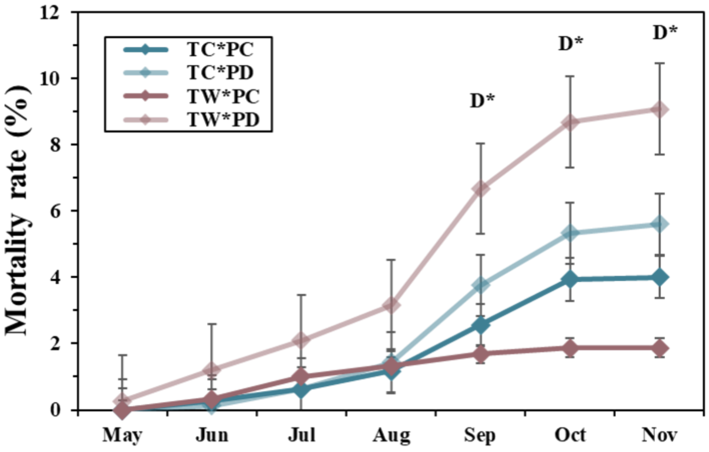

Fig. 4: Mortality of *Larix kaempferi* seedlings in 2020. Abbreviations of the plots are as in Fig. 1. Error bars are the standard errors of the means. Asterisk (*) symbol indicates a significant difference by the drought treatment (*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$).

Discussion

Our findings support the hypothesis that the drought treatment stimulates the final mortality rate (Table 1; Fig. 4). These results are similar to those of a previous study that showed El Niño-related drought of 1982-1983 was associated with elevated mortality rates (Gilbert et al. 2001). In general, soil moisture conditions are very important for the survival of seedlings in the early stage, and in the case of anisohydric plants, stomatal closure does not occur even during the drying period, so the leaf moisture potential is maintained high (Kwon et al. 2020). Our findings suggest that *L. kaempferi* is thought to show anisohydric characteristics (Kwon et al. 2020), and under reduced moisture conditions, the survival rate was lowered by continuing gas exchange without closing the stomata until death due to water loss.

Contrary to our hypothesis, the warming treatment did not significantly stimulate the final mortality rate (Fig. 4). Similar effects of increased temperature on the mortality rate of seedlings have been previously reported, the seedling survival rate of *Pinus densiflora* showed no significant difference by experimental warming increased by 3 °C (Cho et al. 2014; Kwon et al. 2020). The increased level of temperature in this study may have been insufficient to induce substantial changes in the mortality rate. In addition, the warming treatment was less persistent than the drought treatment on seedlings.

Our data support the hypothesis that the warming and drought treatments restrain seedling height and root collar diameter increments, but this was confined to immediately after the treatment. In our experiment, seedling height increment and root collar diameter increment were highest under controlled conditions in June (immediately after the treatment) and were reduced under the warming and drought treatments, which is consistent with a prior research investigating *Abies fabri* (Yang et al. 2013). This suggests that our warming and drought treatments induced heat and water stress in *L. kaempferi* seedlings. However, the analyses of seedling height, root collar diameter, and biomass accumulation after five months of treatments revealed that seedlings exposed to the combined treatment had the highest mortality rates but showed the highest growth. Similar results were found by Geange et al. (2020) in *Aciphylla glacialis*. Environmental stress significantly increased seedling mortality rate but survived seedlings grew greater than their counterparts.

The positive effects of environmental stress on plant growth have been poorly discussed in the literature, and the mechanisms are not well understood (Lin et al. 2007). The higher growth in TW*PD might be due to the overcompensation (Correia et al. 2018) for the disappearance of the stressful treatments and the low competition effect (Alexander and Mihail 2000) of the surviving seedlings. Overcompensation phenomenon is normally related to a so-called hormetic effect to a disruption in the homeostasis of the organism (Aina et al. 1997), which were observed for animals, plants, and cell studies (Von Zglinicki et al. 1992; Beyersmann and Hechtenberg 1997; Agathokleous et al. 2020). Seedlings of TW*PD experienced low intraspecific competition through the mortality rate increased and thus were able to grow larger. Especially, intraspecific competition is reported to reduce biomass production in plants by different investigators (Kleunen et al. 2001, Wang et al. 2005). An increase in plant density may cause an asymmetric frequency distribution of plants, which leads to size variation among plants (Drake and Ungar 1989). For example, if there is competition for water, individuals with larger roots may reduce water available to individuals with smaller roots and as a result, their growth is suppressed. Furthermore, in a symmetrical competitive response, all individuals have an equal decline in biomass production (Wang et al. 2005). Horner et al. (2009) found that the highest density stands were dominated by slender trees, whereas the lowest density stands produced distributions with a wider range of stem diameters and higher mean and maximum stem diameter. Moreover, few studies have shown that high temperature and drought stresses could trigger a series of physio-biochemical compensation in plants. Han et al. (2018) found that the net photosynthetic rate, stomatal conductance, soluble protein, malondialdehyde, and chlorophyll content increased, at 6-9 days after high-temperature stress, which were major driving factors for the compensatory growth of Chinese cabbage. Zhou et al. (2011) found that after 6 days of drought stress and rehydration, the proline, soluble protein contents, superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) activities of the seedlings increased significantly. Through high levels of SOD, CAT, and APX enzyme activity, reactive oxygen species can be effectively removed to mitigate membrane damage and membrane lipid peroxidation (Dong et al. 2019).

However, TC*PD, which also had a high mortality rate due to drought stress, did not show as much recovery as TW*PD. Especially, plants growing in the field encounter a number of different co-occurring abiotic stresses that most probably cannot be extrapolated by the sum of the different stresses applied individually, altering plant metabolism in a novel manner (Zandalinas et al. 2016). This might be due to different, sometimes even opposing, signaling pathways induced by combined stress (Suzuki et al. 2014). A similar conclusion has been described for *Eucalyptus globulus* (Correia et al. 2018) under the combined effect of heat and drought and tomato (Rivero et al. 2014) under the combined effect of heat and salt. These findings demonstrate the superior stress resistance and resilience of *L. kaempferi*, even during their mortality rate increased.

Conclusions/ wider implications of findings

In conclusion, our study demonstrates that despite the high mortality and growth decrease during treatment period, seedlings subjected to high temperature and drought combined stress showed short-term high levels of resilience than seedlings subjected to a single stress. However, these recovery mechanisms do not necessarily lead to the positive effect of early spring warming and drought on *L. kaempferi* seedlings. More extreme and persistent stresses are likely to result in the reduction of growth with higher mortality rates. In order to accurately predict stress response dynamics under climate change, further studies should be conducted on various stress levels, along with studies on physiological responses and protection mechanisms such as the antioxidant systems.

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